NORTH CAROLINA MARINE ALGAE. VIII. THE REPRODUCTIVE MORPHOLOGY OF CALLITHAMNION CORDATUM BORGESEN (RHODOPHYTA, CERAMIACEAE)

CRAIG W. SCHNEIDER

Since the time of its collection in March, 1906 and its description from 27m in the sound off Cruz Bay in the Virgin Islands (Børgesen, 1909), only one previous report (Børgesen, 1915) has added information to the morphology of Callithamnion cordatum Børgesen, and that contained only vegetative data. This taxon has subsequently been collected only from the continental shelves of Bermuda (Collins & Hervey, 1917; Howe, 19181), Southern California and Pacific Baja California (both as Aglaothamnion cordatum (Børg.) Feldm.-Maz.; Abbott & Hollenberg, 1976; Dawson, 1962), Florida (Humm, 1964; Croley & Dawes, 1970), Curazao (Díaz-Piferrer, 1964), and Antigua (Taylor, 1969).

During a June 9, 1975 Scuba dive on the wreck of the cargo ship Suloide² in Onslow Bay, North Carolina, this writer observed a great amount of this pale pink species on macroscopic algae as well

as on the hard substrate of the sunken ship. Male, female, and tetrasporic specimens were all present (CWS 990).

Two tiny samples of Callithamnion cordatum had been collected previously by dredging from R/V Eastward in Onslow Bay³ (June 22, 1970, \mathcal{F} ; June 24, 1971, \mathcal{Q}) and several plants most recently by Scuba4 (CWS 78-5-15, June 16, 1978, ⊕, ♂). Subsequent dives on the Suloide in June, as well as other months of 1976, 1977, and 1978 have provided only one additional collection of C. cordatum (CWS #78-3-6, June 11, 1978, \oplus). This report adds yet another offshore species to the flora of North Carolina (Searles & Schneider, 1978).

MATERIALS AND METHODS

The collections of Callithamnion cordatum made by diving and

¹Taylor (1960) erroneously reported this as Howe (1920), in which no report of C. cordatum was made.

²WR-13, 34° 32'48"N, 76° 53'43"W, depth top 13m, bottom 21.5m, sunk March 26, 1943.

³Station No. 14553, June 22, 1970, 34° 19.6'N, 77° 18.2'W, depth 19m, &; Sta. No. 17309, June 24, 1971, 34° 19.4'N, 76° 53.2'W, depth 28m, Q.

4CWS 78-5, June 16, 1978, 34° 19.0'N, 76° 53.0'W, depth 32m, ⊕, ∂.

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dredging (see Schneider, 1976) were preserved in 10% formalinseawater. For microscopic examination, the specimens were stained with 1% aniline blue, fixed with 1% HCl, and mounted in 20% Karo-distilled water with phenol added as a preservative. Drawings were made utilizing a camera lucida. Comparative dried material was borrowed from the Botanical Museum, Copenhagen (including type material) and the New York Botanical Garden (Collins & Hervey, as well as Børgesen material). The Carolina specimens are liquid preserved and are deposited in the Duke University Algal Herbarium and the C. W. Schneider Herbarium at Trinity College.

MORPHOLOGY

Vegetative. The Onslow Bay specimens differ slightly from Børgesen descriptions (1909, 1915). These newly collected plants display little, if any, incurving of the branches, as opposed to the marked curvature as drawn by Børgesen (Fig. 202, 1915). Because the type and other borrowed material was dried, it was difficult to discern whether the Virgin Island and Bermudan specimens always showed the habit elucidated by Børgesen (1909, 1915). In the lower portions of the main axis, the large cells have large pit discs (to 25 μ m) between them (pd, Fig. 1). Børgesen (1915) observed that unicellular hairs are found most abundantly in the younger portions of the plants (Fig. 2); however, I have observed hairs of nearly twice the length he previously reported, to 250 µm long. Callithamnion cordatum can easily be distinguished from C. byssoides Arnott ex Harvey in Hooker, the commoner species of this genus in North Carolina from the intertidal, as well as shelf waters (Schneider, 1974, 1976). C. cordatum branches alternately in the lowermost portions and pseudodichotomously or its near approach above, including the ultimate segments. C. byssoides is alternately pinnately branched throughout (Harvey, 1846, pl. 262; Taylor, 1960) unlike the habit illustration provided by Børgesen (1915). The overall habit of C. byssoides is plumose and much more dense than

that of C. cordatum.

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Tetrasporic plants. Tetrasporangia are borne singly, or occasionally in pairs (Fig. 3) or groups of three, distally and adaxially on cells of ultimate or penultimate branches, usually in the upper portions of the plant. The sporangia are obovate (rarely orbicular),

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evenly or unequally tetrahedrally divided, and 47–50 μ m in diameter (including the cell wall) by 55–63 μ m long. Although Børgesen (1909) reported sporangia as about 27 × 40 μ m (probably not including the cell wall), I have observed a range of 37–43 × 52–55 μ m from his Virgin Island specimens. This non-overlap of figures might show significant population differences, but it should be recognized that the Carolina plants were liquid preserved and the Virgin Island plants were dried. Usually, rehydration of dried specimens does not restore full natural cell sizes. No tetrasporangia were found on gametophytic plants from Onslow Bay, as was reported by Børgesen (1909).



50 M

Figures 1-6. Callithamnion cordatum Borg. 1. Two lower axial cells of the main axis with a pit disc (pd) between them. 2. Tip segment with a terminal hair (h) and hair cell (hc). 3. Tetrasporangial mother cell with a mature sporangium (ms) and a second tetrasporangial initial (ti). 4-6. Development of the spermatangial cluster and spermatia (s) from the dividing spermatangial initial (si).

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Male plants. Callithamnion cordatum is dioecious. Spermatangia are always produced distally and adaxially on cells of ultimate or penultimate branches of Onslow Bay plants. The developmental sequence from the spermatangial initial cell to spermatia (Figs. 4-6) is similar to the ontogenetic scheme most recently elucidated for other species of Callithamnion by Tazawa (1975). Division of the spermatangial initial is distal in early stages (Figures 4-5), but eventually divisions are produced in all directions of 1 plane, making the cluster hemispherical. Each cluster is enclosed in a gelatinous matrix (Fig. 6). Occasionally two spermatangial clusters become confluent due to the more abbreviated branch cells in ultimate portions of the plant, however, the spermatangial initial is always cut off in a distal position. In contrast to North Carolina plants, Dawson (1962) illustrates median, as well as distal, spermatangial clusters from Pacific Baja specimens. Dawson does not discuss or illustrate the position of the spermatangial initial. The development of the spermatangial cluster by repeated division of a single initial, specially formed from a vegetative cell and not incorporated within the plant's vegetative structure, was unique for Callithamnion among the many genera studied by Tazawa (1975).

Female plants. Although Børgesen (1909) illustrated the 4-celled carpogonial branch and the mature cordate carposporophytes of *Callithamnion cordatum*, the pre- and post-fertilization stages of the female system were not additionally illustrated or elucidated. Onslow Bay specimens allowed for a complete study of these features (Figures 7–18).

Early development of the procarp occurs only a few cells from the

Figures 7–15. Callithamnion cordatum Borg. 7. First auxiliary mother cell (am) being cut off the fertile axial cell (fac). 8. Supporting cell (su) and first 3 cells of carpogonial branch (c1-c3). The second auxiliary mother cell cut off in an adjacent position. 9. Four celled straight carpogonial branch (cb) with trichogyne (t). 10 & 11. Carpogonial branches on supporting cells (su) and fertile axial cells (fac) in a curved arrangement. Carpogonia (cp) with trichogynes (t). 12. Post-fertilization carpogonial branch, the carpogonium (cp) without a trichogyne. Auxiliary cells (a) cut off the basal cells (bc). 13. Young gonimoblast (yg) cut off the gonimoblast initial (gi) of one auxiliary cell (a). Second auxiliary cell branch not yet producing gonimoblasts. Basal cell = bc. 14. Primary gonimoblasts (pg) developing while carpogonial branch (cb) and divided carpogonium (dcp) remain intact. Note early fusion in right hand gonimoblast. 15. Branching pattern of 1° gonimolobes. Basal septum (bs) cut off the auxiliary cell (a).



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apex of the branches. An auxiliary mother cell (am), or pericentral cell (Fritsch, 1945), is cut off from an intercalary fertile axial cell, usually shorter in length than the cells contiguous with it (fac, Fig. 7). Shortly thereafter, this auxiliary mother cell acts as a supporting cell (su) and sequentially cuts off a four-celled carpogonial branch (c1-c3, Fig. 8; cb, Figs. 9-11). This fertile branch is cut off in a straight (Fig. 9) or curved arrangement (Figs. 10-11). Trichogynes of terminal carpogonia (cp) are oriented in various directions relative to the vegetative axis. The second auxiliary mother cell is cut off the same fertile axial cell in an adjacent position early in carpogonial branch development, similar in sequence to one other species, Callithamnion reductum Baardseth (1941). This timing is, however, inconsistent with typical Callithamnion development (Oltmanns, 1898; Westbrook, 1927), where both auxiliary mother cells are cut off prior to carpogonial branch formation. Once fertilization occurs, the trichogyne withers and the auxiliary mother cells divide unequally into distal auxiliary cells (a) and proximal basal cells (bc, Fig. 12). The fertilized carpogonium enlarges and equally divides longitudinally into two cells (dcp, Figs. 14-15). In the typical postfertilization Callithamnion scheme (Oltmanns, 1898 for C. corymbosum (J. E. Sm.) C. Ag.), these divided carpogonial cells each form a connecting cell which ultimately fuses with the respective auxiliary cell. I have not observed such connecting cells for C. cordatum, but do not doubt their existence. Once the diploid nucleus is received, each auxiliary cell forms a primary (1°) gonimoblast, though not at the same time (yg, Figure 13). Cells of the carpogonial branch usually persist into the gonimoblast stage (Figures 14-15). As the gonimoblasts form distally, the haploid auxiliary cell nucleus, no longer necessary for post-fertilization development, is isolated in a basal septum (bs, Figure 15). The basal and auxiliary cells begin to fuse as the 1° gonimoblast forms (Figure 14) and these eventually fuse with a few early gonimoblast cells to form a large fusion cell (fc, Figures 16-17). Sometime after the 1° gonimolobe has developed, a secondary (2°) gonimolobe is produced from a differentiated, unfused primary gonimoblast member (sg, Figures 16-17). The 1° and 2° gonimoblasts are ovoid (Figures 16-17) and each cell of the gonimolobe eventually becomes a viable carpospore. Carpospores of the 1° gonimolobe range in size from 30-50 µm in diameter with 2° gonimolobe carpospores being somewhat smaller. The carposporophyte, then, from its respective fertile axial cell is composed of four major

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gonimolobes (Fig. 18). Each half is often cordate in shape (Børgesen, 1909, Figures 5G, 6; 1915, Figures 202, 203G, 204) but occasionally they are irregularly ovoid (Figure 18).

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DISCUSSION

The reproductive ontogeny for the genus Callithamnion was out-

lined by Oltmanns (1898) and later summarized by Fritsch (1945). This typical sequence of pre- and post-fertilization stages has been



Figures 16-18. Callithamnion cordatum Børg. 16. Primary (pg) and secondary gonimoblasts (sg), early fusion cell formation (fc). 17. Later carposporophyte development with 1° (pg) and 2° (sg) gonimolobes and late fusion cells (fc). 18. Mature irregularly ovoid lobes of carposporophyte.

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elucidated for a number of Callithamnion species by Kylin (1923), Rosenvinge (1923), Westbrook (1927, 1930), and Levring (1937). One taxon, C. reductum has been shown to deviate distinctly from this typical scheme by producing only one auxiliary cell, that being derived from the auxiliary mother cell opposite to the supporting cell which produces the carpogonial branch (Baardseth, 1941). Although C. cordatum parallels the typical Oltmanns' stages in most respects, this species initiates its auxiliary mother cells in a fashion similar to C. reductum. Callithamnion cordatum was transferred to a newly erected genus, Aglaothamnion Feldmann-Mazoyer (1941), a change accepted by Dawson (1962) and Abbott and Hollenberg (1976), but not by all (e.g., Taylor, 1960). The straight/curved carpogonial branches and irregular carposporophytes of C. cordatum support previous criticisms (Harris, 1962) of some criteria on which Aglaothamnion was based. C. cordatum would fall between the two genera, Callithamnion and Aglaothamnion. Further data on the nuclear status of mature C. cordatum vegetative cells are required to relate the present situation to all the criteria used, but this species seems to support retention of Callithamnion sensu lato. The report of Callithamnion cordatum from North Carolina adds another northernmost distributional record for an algal species centered in the Caribbean and another species to the subtropical offshore flora of the Carolinas (Schneider, 1976). This species is known from deep water throughout its range, with few exceptions from shallow waters (Díaz-Piferrer, 1964; Humm, 1964). Including this report, 22 species of Ceramiales have now been added to the North Carolina flora since the offshore project began in 1968 (Schneider, 1975). As to the circumstances surrounding the abundance of C. cordatum in June, 1975 and its subsequent disappearance from the Suloide nothing is known.

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DEPARTMENT OF BOTANY TRINITY COLLEGE HARTFORD, CONNECTICUT 06106

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